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A REVIEW OF THE *PHYLLOMEDUSA BUCKLEYI*
GROUP (ANURA: HYLIDAE)

By

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The leaf-frogs of the subfamily Phyllomedusinae are among the most bizarre residents of the Neotropics. Currently, the group consists of three genera—*Agalychnis*, *Pachymedusa*, and *Phyllomedusa* (Duellman, 1968). Members of the genus *Agalychnis* inhabit humid lowland and montane forests of Middle America and northwestern South America. This genus includes eight species, most with brilliant flash colors and well-developed interdigital webbing. The monotypic *Pachymedusa* has a robust body and occurs in the dry lowlands of western México. The genus *Phyllomedusa*—an unnatural assemblage of about 30 species—is primarily South American; only two species are known from Central America (see Duellman, 1977, for list of species). The more specialized species of *Phyllomedusa* have highly modified, grasping feet, and demonstrate a walking, rather than the leaping gait characteristic of *Agalychnis*.

Possibly one extreme in morphology among phyllomedusines is exemplified in *Phyllomedusa sauvagei*, a plain, xeric-adapted species with enormous parotoid glands and specialized grasping feet with no webbing. In contrast, *Agalychnis callidryas*, occurring in humid tropical lowlands, has gaudy flash colors and extensively webbed hands and feet. Between these extremes is a group of relatively generalized species inhabiting northwestern South America and southern Central America—the *Phyllomedusa buckleyi* group.

The purposes of this paper are 1) to define the *P. buckleyi* group, 2) to diagnose the species, and 3) to present new data and to review the available data on the biology of the species.

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MATERIALS AND METHODS

The systematic studies are based on the examination of 262 preserved frogs, 21 skeletal preparations, 15 lots of tadpoles, two clutches of eggs, and 15 radiographs. Recordings of calls were analyzed with a Vibralyzer (Kay Electric Company). Calls were analyzed and measurements of external morphological characters were taken in the manner described by Duellman (1970). Osteological observations and terminology were based on Trueb (1973, 1977). Statistics were computed in part with the aid of BMDP programs (Dixon, 1975). Webbing formulac were described in the manner of Savage and Heyer (1967), and tadpoles and eggs were staged according to Gosner (1960). Muscle dissections were stained as described by Bock and Shear (1972). Illustrations were executed by means of a Wild M-8 microscope with a camera lucida attachment. Ecological data and color notes were taken from the field notes of William E. Duellman and the author; these are filed in the Museum of Natural History at The University of Kansas. Throughout the text snout-vent length is abbreviated as SVL.

Specimens are referred to by the following abbreviations:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
BYU	Brigham Young University
CAS-SU	California Academy of Sciences
EBRG	Estación Biológica Rancho Grande

FMNH	Field Museum of Natural History
ICN	Instituto de Ciencias Naturales, Bogotá
KU	The University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology
NHRM	Naturhistoriska Riksmuseet, Stockholm
UMMZ	The University of Michigan Museum of Zoology
USC-CRE	University of Southern California
USNM	National Museum of Natural History

SYSTEMATICS

The *Phyllomedusa buckleyi* Group

Definition.—1) Sexual dimorphism in size; SVL to 44.5 mm in males, 54.7 mm in females; 2) hands and feet less than one-fourth webbed; 3) calcars present or not; 4) parotoid gland not differentiated; 5) white dorsal warts present or not; 6) males having thin horny nuptial excrescence; 7) males having single, median subgular vocal sac; 8) first toe shorter than second; 9) palpebrum unpigmented; 10) dorsum uniformly green by day with reddish brown flecks, lacking pattern; 11) flanks bright orange in life, lacking spots or pattern; 12) iris creamy white, with silver to bronze cast; 13) prevomerine teeth present in some individuals of all species, situated on posteromedially directed dentigerous processes; 14) frontoparietal fontanelle exposed as a large oval; 15) quadratojugal present or not; 16) sacral diapophyses widely expanded, with convex edges; 17) posterior portion (*pars scapularis*) of *depressor mandibulae* absent; 18) nektonic tadpoles having oval bodies and moderately deep tail fins; 19) mouths of larvae anteroventral, lacking labial papillae anteromedially; 20) tadpoles having a denticle formula of 2/3.

Content.—Four species: *Phyllomedusa buckleyi* Boulenger, 1882; *P. lemur* Boulenger, 1882; *P. medinai* Funkhouser, 1962; *P. psilopygion* new species.

Distribution.—The combined distributions of the four species include the Cordillera de la Costa in Venezuela, the Caribbean and Pacific slopes of highlands in Panamá and Costa Rica, the Chocó region of Colombia, and the Amazonian slopes of Ecuador, with an altitudinal range of 100 to 1870 m (Figs. 1 and 2).

Remarks.—The frogs of the *P. buckleyi* group most closely resemble some of the small generalized *Phyllomedusa* inhabiting the coastal ranges of southeastern Brasil—*aspera*, *cochranae*, *fimbriata*, *guttata*, and *marginata*. *Phyllomedusa aspera* is too poorly known to warrant further comparison with the *buckleyi* group. According to Izecksohn and da Cruz (1976), *fimbriata* and *marginata* form a natural group; *P. guttata* and *cochranae* form another species-pair on the basis of their specialized larvae (Bokermann, 1966). These

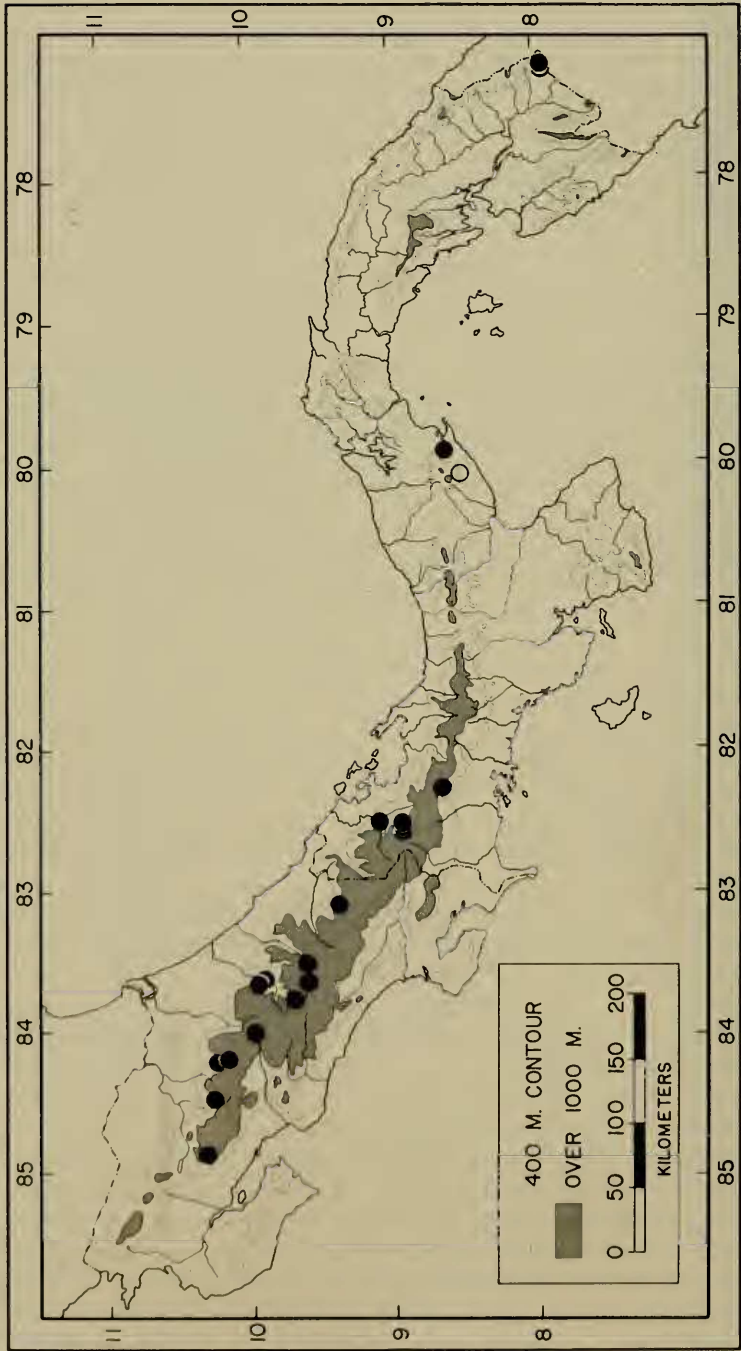


FIG. 1.—Distribution of *Phyllomedusa lemur*. Open circle represents literature record.

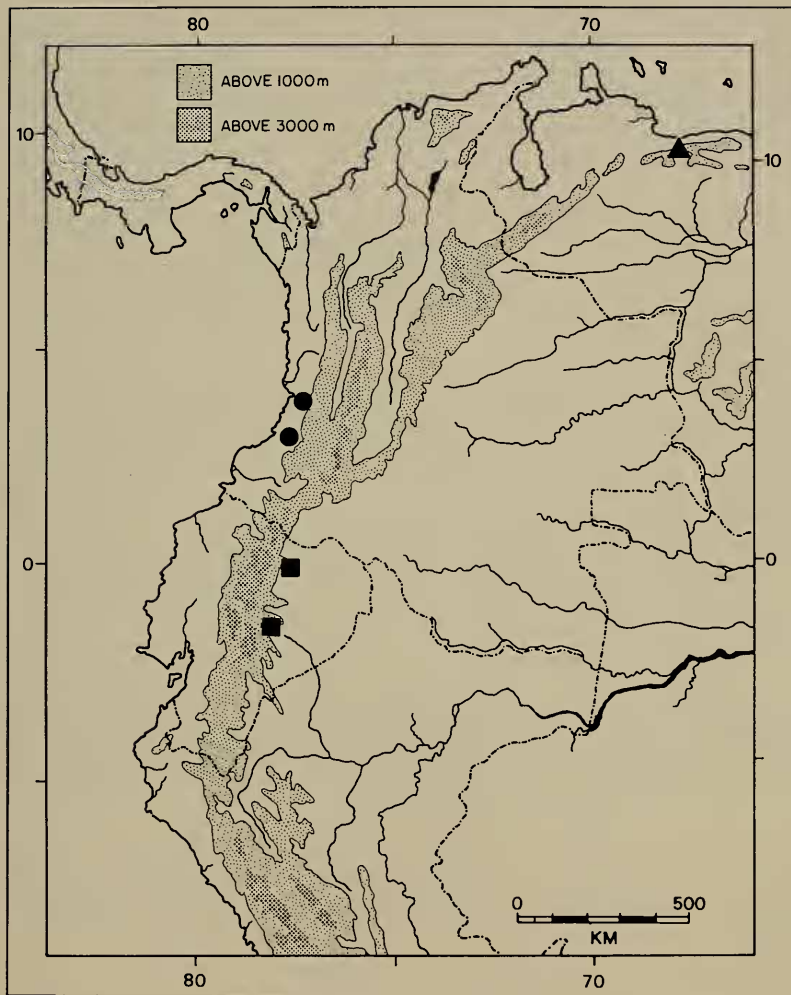


FIG. 2.—Distribution of *Phyllomedusa buckleyi* (squares), *P. psilopygion* (circles), and *P. medinai* (triangle).

stream-adapted larvae, as well as the spotted pattern on the flanks of the adults, separate the *guttata* group from the *buckleyi* group. The *fimbriata* group (*fimbriata* and *marginata*) can be distinguished by the presence of a long, pointed calcar and tadpoles with labial papillae present anteromedially (Lutz and Lutz, 1939); in addition, the feet of *fimbriata* are about one-half webbed. *Phyllomedusa marginata* differs further from the *buckleyi* complex by a bicolored iris and gray to beige flanks (Izecksohn and da Cruz, 1976).

Duellman (1973) referred *Phyllomedusa perinesos* to the *buck-*

leyi group. His conclusions were based on his examination of the only known specimen, the holotype. Material collected subsequently has yielded the following data on *perinesos* that exclude it from the *buckleyi* group: (1) parotoid gland differentiated; (2) posterior portion (*pars scapularis*) of the *depressor mandibulae* present; (3) first toe equal in length to second. These three characters alone ally *perinesos* to the more specialized species of *Phyllomedusa* with grasping feet, such as *tarsius* and *tomopterna*. In members of the *buckleyi* group the first toe is distinctly shorter than the second; as it is in *Agalychnis* and *Pachymedusa*. In skeletal preparations of species of the *buckleyi* group, Metatarsal I is distinctly shorter than Metatarsal II. In species with specialized grasping feet, such as *perinesos*, *tarsius*, *rohdei*, and *sauvagei*, Metatarsal I is equal to, or greater in length than Metatarsal II. In these species the first toe is superficially equal to, or greater in length than the second toe; this condition obviously is derived. Data from Anderson (1978) demonstrate correlative differences in myology of the foot. Thus, on the basis of foot structure, as well as the other characters mentioned above, *perinesos* is excluded from the *buckleyi* group.

Duellman (1970) remarked that possibly *lemur* and *medinai* are conspecific. The various lines of evidence discussed below do not support this suggestion.

Duellman (1968, 1969) suggested that the *buckleyi* group should be accorded generic status. From my investigations of phyllomedusines, it is clear that the *buckleyi* group does not belong in the genus *Phyllomedusa*; however, the proper generic allocation of these unspecialized frogs must await the completion of studies on other phyllomedusines now in progress.

Within the *buckleyi* group, *buckleyi* and *medinai* are phenetically most similar; *lemur* and *psilopygion* closely resemble each other. As will be seen in the following sections, these similarities are based on superficial similarity and are not necessarily indicative of relationship.

ANALYSIS OF CHARACTERS

External Morphology

Size and Proportions.—Pertinent measurements and ratios are given in Tables 1 and 2. The species of the *P. buckleyi* group are moderate-sized frogs. *Phyllomedusa buckleyi* is the largest (SVL of females to 54.7 mm); *P. lemur* is the smallest—females from Tapantí, Costa Rica attain a SVL of 41.6 mm. *Phyllomedusa lemur* also exhibits a trend for increase in size from west to east (Table 3). The largest specimen of *lemur* examined is a female having a SVL of 52.7 mm.

For each ratio in Table 2, a Kruskal-Wallis analysis of variance

TABLE 1.—Measurements of species of the *Phyllomedusa buckleyi* group. Abbreviations: FOOT, foot length; HLEN, head length; HWID, head width; SVL, snout-vent length; TIB, tibia length; TYMP, tympanum diameter. Observed range given in parentheses below mean and one standard deviation, in mm.

Species	Sex	n	SVL	TIB	FOOT	HLEN	HWID	TYMP
<i>P. buckleyi</i>	♂	21	42.6 ± 1.392 (39.3-44.5)	21.1 ± 0.740 (19.7-22.2)	15.6 ± 0.670 (13.7-17.0)	15.4 ± 0.880 (13.3-17.0)	14.0 ± 0.579 (13.1-15.8)	1.9 ± 0.146 (1.7-2.2)
	♀	7	52.4 ± 2.078 (50.0-54.7)	26.8 ± 3.058 (25.5-28.6)	19.9 ± 1.506 (17.8-22.4)	18.8 ± 0.788 (17.9-20.1)	17.0 ± 0.715 (16.1-17.8)	2.3 ± 0.162 (2.0-2.5)
<i>P. lemur</i>	♂	25	32.4 ± 1.420 (30.1-34.7)	16.7 ± 0.837 (14.7-18.4)	11.1 ± 0.607 (9.8-12.0)	10.8 ± 0.474 (9.8-11.6)	10.1 ± 0.510 (9.2-11.0)	1.6 ± 0.151 (1.3-1.9)
	♀	2	40.6 (39.5-41.6)	21.8 (21.7-21.9)	13.8 (13.7-13.8)	13.2 (12.7-13.7)	12.2 (12.0-12.4)	2.0 (2.0)
<i>P. medinae</i>	♂	3	40.7 ± 2.190 (39.0-43.2)	19.7 ± 0.808 (18.2-20.2)	14.2 ± 0.819 (14.0-15.1)	14.5 ± 0.838 (14.0-15.5)	13.9 ± 0.987 (13.2-15.0)	1.9 ± 0.173 (1.7-2.0)
	♀	4	47.2 ± 0.619 (46.4-47.9)	23.3 ± 0.287 (22.9-23.5)	17.0 ± 0.619 (16.1-17.5)	16.5 ± 0.476 (16.0-17.0)	16.1 ± 0.171 (15.9-16.3)	2.1 ± 0.126 (1.9-2.2)
<i>P. psilopygion</i>	♂	6	40.8 ± 1.220 (38.7-42.0)	20.3 ± 0.717 (19.3-21.0)	13.2 ± 0.314 (12.8-13.7)	15.0 ± 0.612 (14.0-15.8)	14.0 ± 0.437 (13.4-14.5)	1.8 ± 0.172 (1.7-2.2)
	♀	2	46.4 (45.5-47.3)	22.7 (21.5-23.9)	14.8 (13.1-16.4)	16.3 (15.3-17.2)	15.1 (14.8-15.3)	2.8 (2.5-3.1)

TABLE 2.—Proportions of measurements of males in the *Phyllomedusa buckleyi* group. Abbreviations as in Table 1. Values express as percentages; range given in parentheses below mean.

Species	n	TIB/SVL	FOOT/SVL	HLEN/SVL	HWID/SVL
<i>P. buckleyi</i>	20	49.4 (46.2-51.8)	36.6 (33.0-38.7)	36.4 (31.4-38.6)	32.5 (30.8-34.2)
<i>P. lemur</i>	20	51.3 (48.3-55.2)	34.5 (32.0-36.8)	33.0 (31.2-35.7)	31.5 (29.4-34.9)
<i>P. medinae</i>	3	47.3 (46.8-48.2)	34.9 (34.6-35.0)	35.7 (35.0-36.2)	34.0 (33.0-34.7)
<i>P. psilopygion</i>	6	49.8 (47.0-50.7)	32.4 (32.1-33.1)	36.9 (36.2-37.6)	34.2 (32.3-35.1)

(Conover, 1971) was run among the species (males only). For each ratio the null hypothesis—that a ratio was the same in all species—was rejected ($P < 0.001$). A multiple range test for ranked data (Dunn, 1964) was performed next for each ratio (Table 4).

Coloration.—The group is characterized by a uniformly green dorsum (by day) with bright orange concealed surfaces of the limbs and flanks, bearing no spots or pattern. The coloration alone sets the group apart from other phyllomedusines. By night the dorsum is brown, as in some *Agalychnis*. The venter is creamy white with no markings. The iris is off-white with a silver to bronze cast. A clear palpebrum distinguishes the group from *Pachymedusa* and *Agalychnis* (except *calcarifer* and *craspedopus*). Some individuals of *medinai*, *psilopygion*, and *buckleyi* bear dorsal warts; the black outer border seen on the warts of some *Agalychnis* is lacking. *Phyllomedusa lemur* has no dorsal warts. There is no ontogenetic change in color in those species for which the young are known.

Skin.—The dorsal skin is smooth, with a slight shagreen, in all species; the belly skin is granular. Some specimens of *buckleyi* develop faint tubercles on the hind limbs and loreal region; *P. psilopygion* and *buckleyi* bear small calcars. The grossly thickened and well-differentiated parotoid glands seen in more specialized *Phyllomedusa* are absent from this group, as they are from *Pachymedusa* and all *Agalychnis*.

Hands and Feet.—The hands and feet are less than one-fourth webbed (Table 5). *Phyllomedusa medinai* has the greatest amount of webbing (Fig. 3); *buckleyi* has slightly less (see Duellman, 1969, for illustration). *Phyllomedusa lemur* bears only traces of webbing, (see Duellman, 1970, for illustration) as does *psilopygion* (Fig. 3). The slightly enlarged prepollax bears a thin horny nuptial excrescence in breeding males. A small, round outer metatarsal tubercle is sometimes present in *buckleyi* and *medinai*, but absent in the other species. A small, oval inner metatarsal tubercle is uniformly present. The first toe is shorter than the second. The discs on the fingers and toes are relatively larger in *medinai* and *buckleyi* than in *lemur*.

Osteology

Cranium.—The skulls are moderately broad and flat; they lack exostosis, co-ossification, and casquing (Figs. 4 and 5). *Phyllomedusa psilopygion* exhibits the weakest overall ossification. In *psilopygion* and *medinai* the skull is slightly wider than it is long; in *buckleyi* and *lemur* the width is about the same as the length. Each skull is about one-third as high as long. In dorsal view, the snout is acutely rounded—that portion of the maxilla anterior to the palatines is almost straight. The skull of *psilopygion* is the largest in relative size.

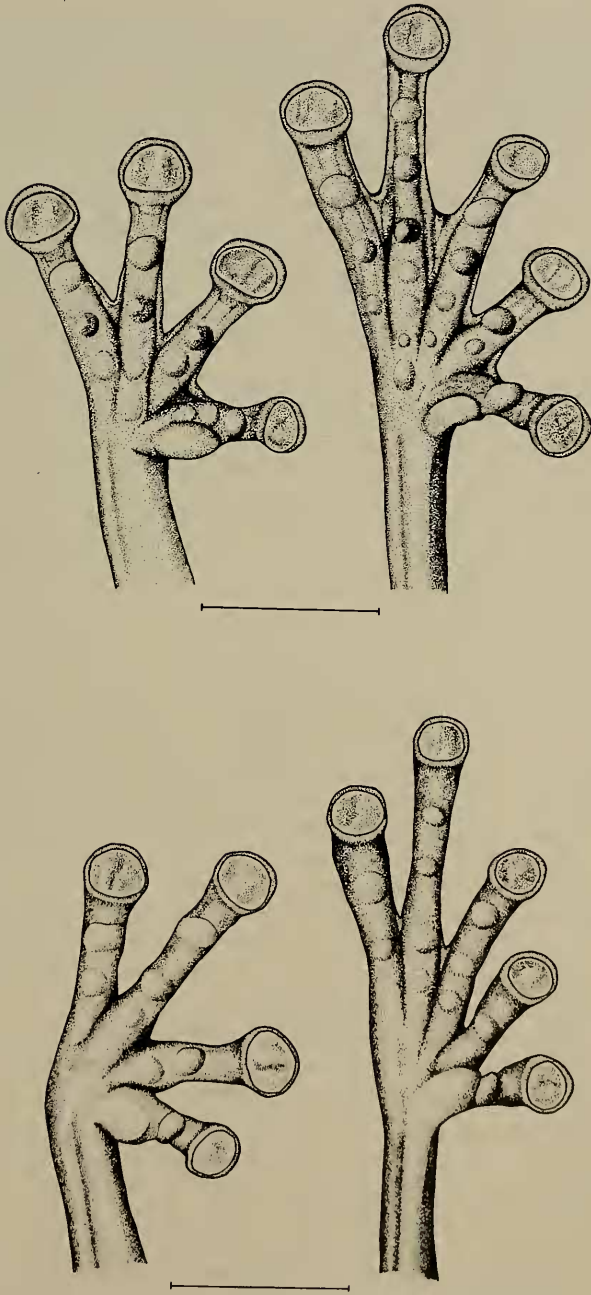


FIG. 3.—Top: Hand and foot of *Phyllomedusa medinai*, KU 167187, female. Bottom: Hand and foot of *P. psilopygion*, KU 169612, female. Line equals 2 cm.

The nasals are moderately large and narrowly separated medially. In *lemur* they are the largest and contact the ossified portion of the sphenethmoid in larger specimens. The nasals are slightly smaller in *psilopygion*; the maxillary processes are narrower than those of *lemur*. The nasals are smallest in *buckleyi* and *medinai*, and are notched on the posterior edge.

The ossified portion of the sphenethmoid is shallow in the group; it is most poorly developed in *psilopygion*. Because the frontoparietals are slender, the exposed frontoparietal fontanelle is a large oval. The frontoparietals diverge slightly in *medinai*, resulting in a greater relative interorbital width in that species. The posterior borders of the frontoparietals are obscured by the irregular ossification patterns on the exoccipital. The exoccipital is poorly ossified in *psilopygion*; it is slightly better developed in the other species. In all species the squamosal articulates with the distal portion of the crista parotica that is cartilaginous. The otic rami of the squamosals are of comparable length in all species. The zygomatic ramus is shortest in *psilopygion*; in the other species the ramus is longer, extending about one-third the distance to the maxillary. The articulation of the squamosal and pterygoid is at approximately the level of the occipital condyles.

Phyllomedusa medinai lacks a quadratojugal (Fig. 5); it is present but poorly ossified in the others. In *buckleyi* and *lemur* the quadratojugal may or may not overlap the maxilla. The maxillae are slender and lack postorbital processes; preorbital processes are uniformly present, and do not contact the maxillary processes of the nasals. The pars facialis is very shallow in *psilopygion*, deepest in *lemur*, and moderately developed in *buckleyi* and *medinai*. The pars palatina is narrow in all species, being a little wider than the pars dentalis. Maxillary and premaxillary tooth counts are as follows (n = number of elements, mean in parentheses): *buckleyi*, 88-95 per maxilla (n = 4, 93) and 13-16 per premaxilla (n = 4, 13); *lemur*, 69-96 (n = 6, 79) and 11-15 (n = 6, 13); *medinai*, 100-102 (n = 2, 101) and 14-15 (n = 2, 15); *psilopygion*, 86-93 (n = 2, 90) and 12-12 (n = 2, 12). The great range in maxillary teeth in *lemur* reflects the range of maxillary lengths; there is a direct relationship between the number of teeth and the length of the maxilla.

The septomaxillaries are U-shaped. The alary processes of the premaxillaries are directed dorsally in *lemur* and *psilopygion*, and posterodorsally in *buckleyi* and *medinai*. In all species the length of the alary processes is about the same as the length of the premaxillary tooth row. The processes are notched in all species; they diverge slightly in *buckleyi* and *medinai*. The pars palatina is moderately developed and widens distally in the group. The prominent palatine processes are about one-half the length of the premaxillary tooth row.

The pterygoids are uniformly triradiate and weakly developed. The anterior rami terminate one-third of the orbital length from the anterior borders. The medial rami articulate synchondrotically with the anterolateral corners of the otic capsules. The parasphenoids are T-shaped, lacking ridges or odontoids. The alae are acuminate and posterolaterally directed. The cultriform processes are about twice the width of the alae and bear slightly notched termini. In *medinai* the cultriform process reaches almost to the level of the palatines; in the others it is slightly shorter and barely overlaps the ossified portion of the sphenethmoid. In ventral view the ossification of the sphenethmoid in all species extends to the midlevel of the orbit.

The slender palatines are widened and flattened distally. *Phyllomedusa lemur* possesses thin, anteromedially directed processes that originate from the anterior border of the distal ends of the palatines. These peculiar processes appear to reinforce the anterolateral margins of the internal nares (Fig. 5). In all species, the palatines are separated medially by a distance equal to the width of the sphenethmoid.

The prevomers are small, with thin lateral processes forming the anterior and medial borders of the choanae. The dentigerous processes are short and oriented posteromedially ($\setminus/\$); they are almost perpendicular to the midline in *medinai*.

All specimens of *lemur* from localities west of Moravia de Turrialba, Costa Rica, lack dentigerous processes and prevomerine teeth. Specimens from Moravia de Turrialba are variable; dentigerous processes and/or teeth are sometimes present. Specimens from localities east of Moravia de Turrialba have prevomerine teeth more often than not. The presence of prevomerine teeth and dentigerous processes in *lemur* is correlated roughly with the SVL of the specimen, for there exists a trend for increase in SVL from west to east (Table 3). In *buckleyi*, *medinai*, and *psilopygion*, dentigerous processes are invariably present; teeth may be absent. The prevomerine tooth counts for the species are as follows (range, mean in parentheses, n = number of elements): *buckleyi*, 0-6 (4, n = 56); *medinai*, 0-4 (2, n = 14); *lemur*, 0-5 (2, n = 30); *psilopygion*, 0-5 (2, n = 14). The presence of prevomerine teeth in *medinai* and *lemur* has not been reported previously by other authors (Funkhouser, 1962; Duellman, 1969).

The occipital condyles are widely separated and stalked. Columellae are slender, and present in all species.

The mandibles lack ridges or odontoids. The dentaries and angulars are moderately developed; a small coronoid process is present. The mentomeckelian elements are poorly ossified.

Vertebral Column.—Eight presacral vertebrae are uniformly present. The cervical cotyles are widely separated in all species.

TABLE 3.—Geographic variation in size and presence of prevomerine teeth in *Phyllomedusa lemur*. For SVL, ranges in parentheses after means, in mm. Teeth present = percentage of *n* with prevomerine teeth present.

Locality	Longitude	sex	<i>n</i>	SVL	Teeth present (%)
Costa Rica: Tapanti	83°48'W	♂	25	32.4 (30.1-34.7)	0
		♀	2	40.6 (39.5-41.6)	0
Costa Rica: Moravia de Turrialba	83°26'W	♂	15	34.2 (30.0-35.7)	47
		♀	6	41.1 (39.8-43.7)	33
Panamá: Río Changuena	82°36'W	♂	4	34.1 (32.2-35.5)	25
		♀	6	44.5 (43.6-46.8)	66
Panamá: Río Chiriquí	82°20'W	♀	2	45.4 (43.7-47.0)	50
Panamá: Cerro Campana	79°56'W	♂	2	39.5 (38.1-40.8)	100
		♀	1	44.0	100
Panamá: Cerro Malí and Cerro Tacarcuna	77°15'W	♂	2	43.2 (42.6-43.5)	100
		♀	2	51.7 (50.6-52.7)	50

The neural arches are low and non-imbricate. Poorly developed neural spines are present only on Presacrals I and II. The width of the transverse processes of Presacral III slightly exceeds the width of the sacral diapophyses in *medinai*, *lemur* and *buckleyi*. In *psilopygion* the widths are subequal. The transverse processes in all species are moderately wide and subequal in width. The profile of the process widths gradually narrows posteriorly. The tips of the transverse processes of Presacrals III–V bear conspicuous bits of calcified cartilage. These are noticeable in both dry and alizarin preparations. The processes of Presacrals III–IV are directed posterolaterally. The processes of Presacral VI are directed only slightly posteriorly; in the remaining vertebrae the processes are anterolaterally directed, the inclination being most pronounced in *lemur*.

The vertebral centra are uniformly procoelous. The sacral diapophyses of all species are widely expanded and articulate over a wide area with the ilial shaft. In *psilopygion* small flanges are present posteriorly at the base of the sacral diapophyses. In all species the coccyx bears no distinct ridge. A bicondylar sacro-coccygeal articulation is present in *buckleyi*, *lemur* and *medinai*. In all specimens of *psilopygion* the coccyx is fused to the sacrum with no trace of a suture. To my knowledge, this is the first report of a fused sacro-coccygeal articulation in the Hylidae (Trueb, 1973).

Pectoral Girdle.—The pectoral girdles are fully arciferal; the sterna are bifurcate and exhibit only traces of calcium deposition. The omosternum is questionably present in *buckleyi* and *lemur* as a small bit of cartilage; it is absent in *medinai* and *psilopygion*. The clavicles are slender and moderately arched; the coracoids are moderately robust and are best developed in *medinai*. Procoracoid cartilage is present in all species; it is most extensive in *medinai*. The epicoracoid cartilages are moderately curved and overlap over most of their length. The scapulae are much longer than the clavicles and are proximally bifurcate in all species. The cleithra are bicapitate distally in *buckleyi* and *medinai*, and uncleft in the others. The suprascapular cartilages are about as long as wide; small amounts of calcium deposition can be noted.

Pelvic Girdle.—The ilia of all species lack any indication of a crest on the shaft. Low dorsal protuberances are present in all species. The lateral preacetabular angle is less than 90° in the group; the interior pelvic angle is about 35° . The acetabular length is greater than the acetabular height. The ischium is moderately expanded; the pubis is poorly ossified.

Myology

The terminology of the following muscle descriptions follows Starrett (1968) and Tyler (1971).

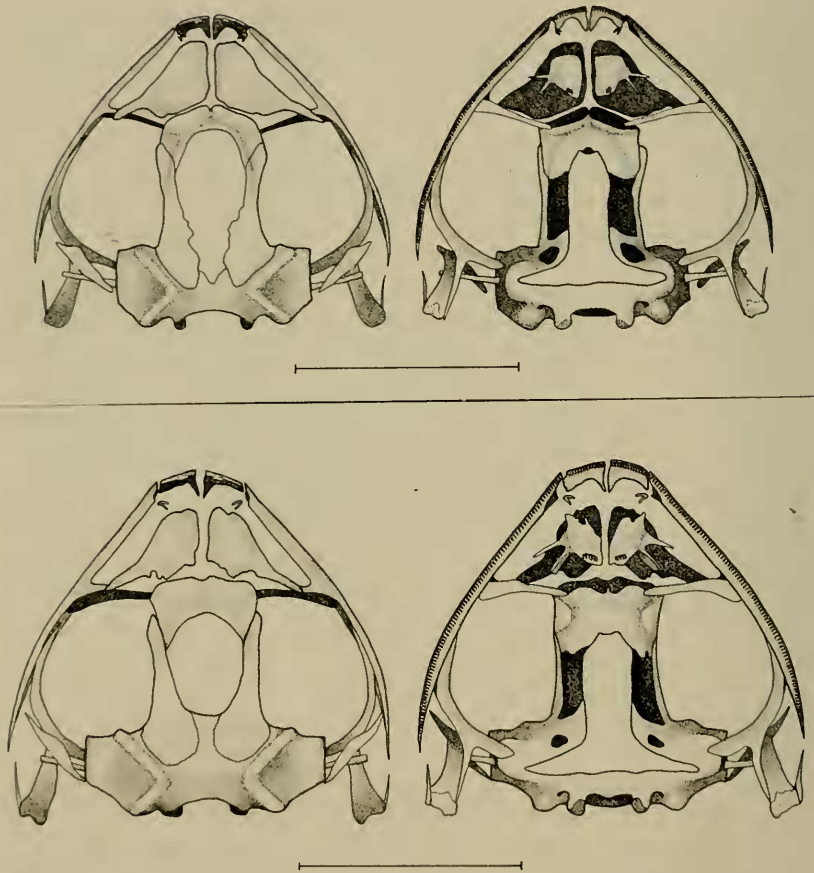


FIG. 4.—Dorsal (left) and ventral (right) views of skulls of *Phyllomedusa psilopygion* (top), KU 169613, male, paratype, and *P. buckleyi* (bottom), KU 179405, male. Line equals 1 cm.

Depressor Musculature.—The main portion of the *depressor mandibulae* originates from the posterior ramus of the squamosal (no fibers arise from the erista parotica) and inserts on the end of the mandible. A smaller slip of the *depressor mandibulae* arises from the medial aspect of the posteroventral portion of the tympanic ring cartilage and also inserts on the end of the mandible. No slips of the *depressor mandibulae* arise from the dorsal fascia of the suprascapula. In Starrett's code, the musculature can be characterized as SQat.

Adductor Musculature.—The *adductor mandibulae externus lateralis* is present in all four species, and originates from the quadratojugal and the base of the squamosal, except in *medinai*. The center of ossification is lost from the quadratojugal in *medinai*,

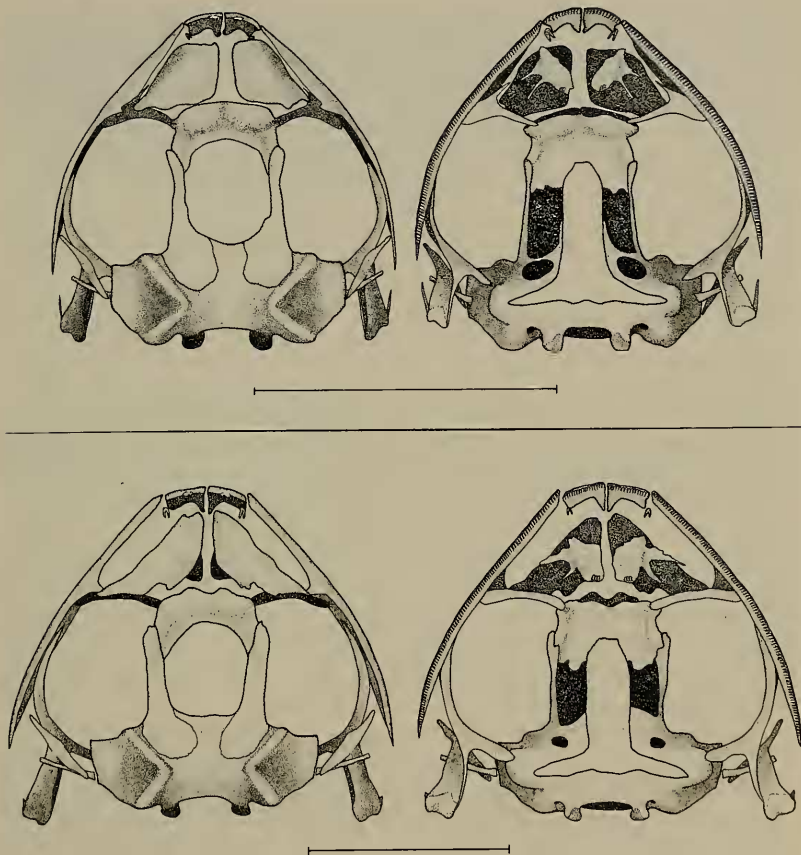


FIG. 5.—Dorsal (left) and ventral (right) views of skulls of *Phyllomedusa lemur* (top), KU 31707, male, and *P. medinai* (bottom), KU 179407, female. Line equals 1 cm.

and the muscle originates solely from the squamosal. The lateral face of the angular receives the insertion in all species.

The *a.m. externus superficialis* is present and well-developed in all species, and passes laterad to the mandibular branch of the trigeminal nerve (V^3). This muscle originates from anterior ramus and proximal portion of the ventral ramus of the squamosal, and inserts on the lateral face of the mandible.

The *a.m. anterior internus* is present in all species, and takes its origin from the dorsal and lateral surfaces of the frontoparietal, becoming more tendinous where it passes laterad to the anterior ramus of the pterygoid to insert on the medial face of the angular.

Present also in all species is the *a.m. posterior longus*. This most prominent of the adductor series arises from the dorsal surface of the crista parotica and inserts on the angular.

TABLE 4.—Multiple range comparisons of ratios between species, males only. 1 = *P. buckleyi*, 2 = *P. lemur*, 3 = *P. medinai*, 4 = *P. psilopygion*. Sample sizes as in Table 2. The species subtended by lines are not significantly different from each other at the 0.05 level.

Ratio	Multiple range comparison			
TIB/SVL	2	4	1	3
FOOT/SVL	1	3	2	4
HLEN/SVL	4	1	3	2
HWID/SVL	4	3	1	2

Likewise, the *a.m. posterior articularis* is found in all species, originating from the ventral ramus of the squamosal and inserting on the lateral face of the mandible, just posterior to the insertion of the *externus superficialis*.

The *a.m. posterior subexternus* apparently is absent in *medinai* and *psilopygion*. Only one specimen of each species was dissected however. In *buckleyi* and *lemur*, a few muscle fibers appear to originate from the anterior arm of the squamosal and pass ventrad to insert on the lateral face of the mandible. The fibers lie medial to nerve V³, and presumably represent a very reduced *posterior subexternus* muscle.

Intermandibular Musculature.—Tyler (1971) described the intermandibular muscles for a number of phyllomedusines, including *buckleyi* and *lemur*. My dissections of the four species generally agree with Tyler's observations on *buckleyi* and *lemur*. The *submentalis* is small and agraphic; the two halves of the principal element of the *intermandibularis* insert medially on a moderately wide aponeurosis; posterolateral elements of the *intermandibularis* are present; the *interhyoideus* is entire and not lobed. The aforementioned are typical phyllomedusine conditions (Tyler and Davies, 1978).

Tyler (1971) pointed out that when the *posterior subexternus* and the *externus superficialis* are both present, the posterolateral slip of the *intermandibularis* inserts on the *posterior subexternus* via a tendon, and the site of attachment is concealed by the *externus superficialis*. Furthermore, when the *posterior subexternus* is absent, the tendon attaches to the *externus superficialis*. My dissections of *Pachymedusa daenicolor*, *Agalychnis callidryas*, and *Phyllomedusa tarsius* confirm Tyler's observation.

In all members of the *buckleyi* group, the tendon of the posterolateral element inserts on the *externus superficialis*, whether the reduced *posterior subexternus* is present (*buckleyi* and *lemur*) or not (*medinai* and *psilopygion*). Obviously, further analysis is

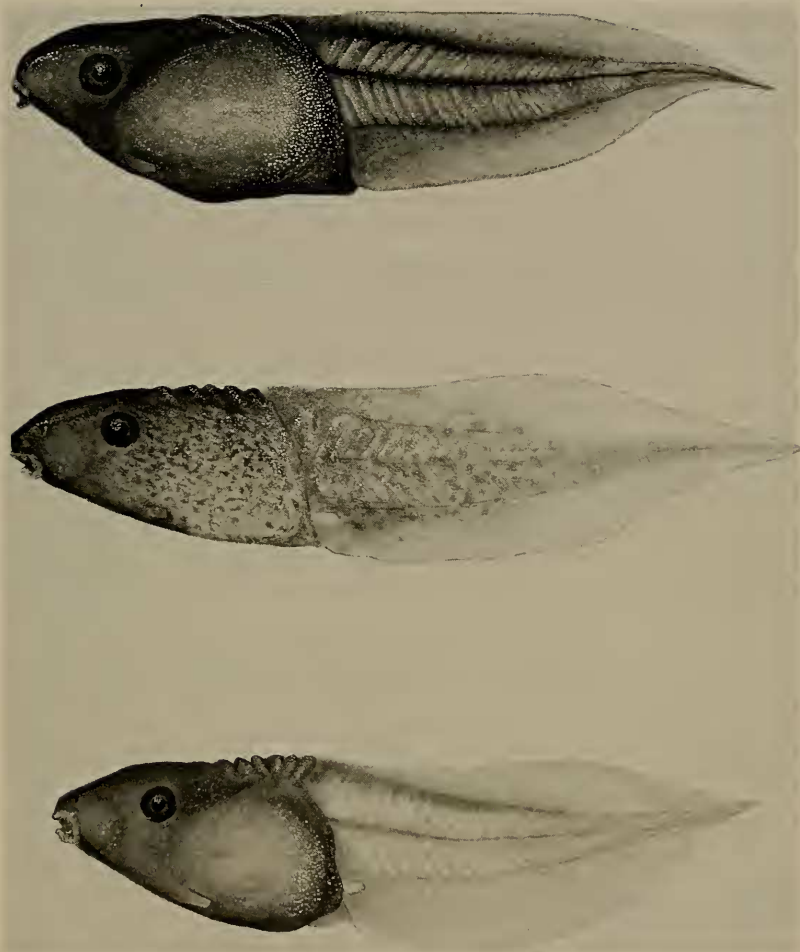


FIG. 6.—Tadpoles of *Phyllomedusa psilopygion* (upper), KU 170213; *P. lemur* (center), USC-CRE 290-9; *P. buckleyi* (lower), KU 143553. $\times 2.5$.

needed to ascertain the extent of ontogenetic variation in the jaw musculature before its utility in systematics can be realized fully.

Tadpoles

Morphology.—In general morphology the tadpoles of the *P. buckleyi* group resemble those of *Agalychnis* and *Pachymedusa* (see Duellman, 1970). The body is oval-shaped; the caudal musculature is slender (Fig. 6). The tail fins narrow gradually to a point. The denticle formula is $2/3$; the second upper row is interrupted medially. The medial portion of the upper lip lacks papillae. The labial papillae are most dense in *lemur*, and least dense in *psilopygion* (Fig. 7).

The chondrocranial elements are visible through the skin in *psilopygion*; this is probably due to a lack of pigment. Since the larvae were collected from a natural grotto, the condition is possibly environmentally induced.

Coloration.—The body of *buckleyi* is grayish brown in preservative; that of *psilopygion* is pale brown. The body of *lemur* is purplish pink with brown mottling. The tail musculature is cream in *buckleyi*, bluish gray in *psilopygion*, and pale cream with brown mottling in *lemur*. Dark brown pigment is present along the dorsal edge of the tail musculature in the three species; the tail fins are transparent in the group.

KEY TO THE SPECIES IN THE *PHYLLOMEDUSA BUCKLEYI* GROUP

1. Snout sloping in lateral view; foot about one-fourth webbed 2
 Snout truncate in lateral view; foot webbing vestigial, barely visible 3
2. Calcar generally present; quadratojugal present *P. buckleyi*
 Calcar absent; quadratojugal absent *P. medinai*
3. Calcar generally present; sacro-coccygeal articulation fused; white dorsal warts usually present; para-anal tubercles absent *P. psilopygion*
 Calcar absent; sacro-coccygeal articulation bicondylar; white dorsal warts never present; para-anal tubercles present *P. lemur*

ACCOUNTS OF SPECIES

Phyllomedusa buckleyi Boulenger

Fig. 8

Phyllomedusa buckleyi Boulenger, 1882:425, pl. 29 [Holotype.—BMNH 80.12.5.230 (RR 1947.2.22.35) from Sarayacu, Provincia de Pastaza, Ecuador].

Phyllomedusa loris Boulenger, 1912:186 [Holotype.—BMNH 1912.11.1:71 (RR 1947.2.25.82) from El Topo, Río Pastaza, Provincia de Tungurahua, Ecuador; synonymy *vide* Duellman, 1969:135].

Phyllomedusa buckleyi—Nieden, 1923:344.

Phyllomedusa loris—Nieden, 1923:344.

Hyla (Hylella) porifera Andersson, 1945:81 [Holotype.—NHRM 1963 from Río Pastaza watershed, Ecuador; synonymy *vide* Duellman, 1969:135].

Phyllomedusa buckleyi—Lutz, 1950:601,619.

Phyllomedusa (Phyllomedusa) loris—Lutz, 1950:601,619.

Phyllomedusa buckleyi—Funkhouser, 1957:26.

Phyllomedusa loris—Funkhouser, 1957:26.

Phyllomedusa buckleyi—Duellman, 1968:6.

Phyllomedusa loris—Duellman, 1968:6.

Phyllomedusa buckleyi—Duellman, 1969:135.

Diagnosis.—*Phyllomedusa buckleyi* differs from other members of the *buckleyi* group by the following combination of characters: 1) modal webbing formula of foot II(2+)—(3.5)III(2.5)—(3.75)IV(3.5)—(2+)V; 2) calcar present; 3) snout sloping in lateral view; 4) para-anal tubercles present; 5) outer metatarsal tubercle usually present; 6) white dorsal warts usually present; 7) quadratojugal present; 8) sacro-coccygeal articulation bicondylar.

Description.—Pertinent measurements and proportions in Tables 1 and 2. Head slightly wider than body; snout short, acutely rounded in dorsal view; in lateral view, sloping and rounded from lip to nostril in both sexes; canthus rostralis rounded, distinct; loreal region concave; lips thin and not flared; nostrils not protuberant, directed laterally; internarial region flat; eyes large and protuberant; pupil vertically elliptical; palpebrum clear; parotoid glands not differentiated; supratympanic fold thin, indistinct, obscuring dorsal edge of tympanum, and up to one-half of tympanum in some; fold extending posteroventrally to a point above the insertion of the arm; tympanum barely distinct, round, separated from eye by distance equal to horizontal diameter of the tympanum.

Axillary membrane absent; upper arm slender; forearm robust; ulnar fold low, indistinct; fingers moderately long; relative length from shortest to longest 1-2-4-3; discs of moderate size, rounded; subarticular tubercles large, subconical; distal tubercle on fourth finger bifid in most specimens; supernumerary tubercles lacking on fingers; palmar tubercle low, diffuse, rounded; prepollex slightly enlarged and bearing thin, horny nuptial excrescence in breeding males; slight rudimentary webbing between the last three fingers (Table 5).

Legs moderately long and slender; small, blunt calcar on heel; a few small tubercles below calcar; inner tarsal fold barely distinct; outer tarsal fold barely distinct, appearing merely as a row of low tubercles in some; toes of moderate length; relative length from shortest to longest 1-2-3-5-4; discs rounded, smaller than those on fingers; inner metatarsal tubercle flattened, low, elliptical; outer metatarsal tubercle small and rounded; webbing absent between first and second toes; rudimentary webbing between second and third, and basal webbing between other toes (Table 5).

Anal opening directed ventrally at midlevel of thighs; short anal flap present; para-anal region tubercular; skin on dorsum minutely granular; white dorsal warts present on some specimens; small granules in loreal and temporal regions; skin on throat, belly and posteroventral surface of thighs distinctly granular; skin elsewhere smooth; tongue lanceolate, notched posteriorly, free for about one-half its length; prevomerine teeth present in most; dentigerous processes of prevomers small, moderately separated medially, oriented posteromedially (∇) at anterior level of elliptical choanae; vocal slits present in males, short, parallel to jaw, extending from posterolateral corner of tongue to corner of mouth; vocal sac single, median, subgular.

Coloration.—In life, dorsum lavender-brown by night; by day dorsum pale green to yellow-green, with purple flecks; dorsal surfaces of toe and finger discs yellowish white with green wash; ventral surfaces of hands and feet flesh-colored; venter cream with

TABLE 5.—Variation in webbing of species of the *Phyllomedusa buckleyi* group. The first and second values in a column are the maximum and minimum; mode in parentheses.

Hand	n	I	II	III	IV	V	
<i>P. buckleyi</i>	15	---	2+ 2.5 (2.5)	2+ 3.5 (3.5)	3- 3+ (3-)	3- 3+ (3-)	
<i>P. lemur</i>	10	---	---	---	3 3+ (3)	3 3+ (3)	
<i>P. medinai</i>	7	---	2+ 2.5 (2+)	3+ 3.5 (3+)	2.75 3 (2.75)	2.75 3 (2.75)	
<i>P. psilopygion</i>	7	---	---	---	---	---	
Foot							
<i>P. buckleyi</i>	15	---	2 2.5 (2+)	3+ 3.75 (3.5)	2+ 2.5 (2.5)	3.5 4- (3.75)	3+ 3.5 (3.5)
<i>P. lemur</i>	10	---	---	---	3- (3+) (3)	4- 4 (4)	4- 4 (4)
<i>P. medinai</i>	7	2+ 2+ 2+	2+ 2.5 (2.25)	3.25 3.5 (3.5)	2+ 2.75 (2+)	3.5 4- (3.5)	3+ 3.25 (3+)
<i>P. psilopygion</i>	7	---	---	---	3- 3 (3-)	4 4+ (4)	2+ 2.5 (2+)

orange wash; throat off-white with pale orange wash; flanks and concealed surfaces bright orange, fading to cream on the edges; ulnar and tarsal fold off-white; anal tubercles off-white; dorsal warts pale yellow; fourth finger green dorsally, fading to pale yellow; third finger dirty yellow; first and second fingers orange dorsally; iris dirty cream; palpebrum clear, upper border slightly pigmented. A newly metamorphosed individual (KU 178850) had the following coloration: dorsal surfaces of body and limbs light green with yellow wash; dorsal surface of toe pads and concealed surfaces dull orange; dorsal wart light yellow; iris off-white; venter fleshy orange; upper lip dirty yellow.

In preservative, dorsal surfaces of body, forearms, thighs, shanks, tarsi, third and fourth fingers, and fourth and fifth toes bluish purple to pale blue; dorsal warts, anal tubercles, ulnar and tarsal fold, white; dark flecks present dorsally; other surfaces cream.

Tadpoles.—About 45 tadpoles were examined, ranging in development from Stage 25 to 41. The range of body lengths is 8.4–24.1 mm; the range of total lengths is 22.1–58.0 mm. A representative tadpole (KU 143553) is illustrated in Fig. 6.

The following description is based on KU 143553 and 166219: body as wide as deep, deepest and widest at two-thirds the length of the body; top of head slightly convex; snout acutely rounded in lateral profile; in dorsal view almost truncate; nostrils dorsolateral, directed anterolaterally; internarial distance less than width of oral disc; eyes dorsolateral and directed laterally; spiracle a flap-like tube, ventral and sinistral to midline; spiracular opening at point about midlength of the body; chondrocranial elements not visible through skin; mouth anteroventral and directed anteriorly; cloacal tube short and dextral to caudal fin; slender caudal musculature tapers gradually to posterior end of fin; myomeres moderately developed; at midlength of the tail the depth of the caudal musculature slightly less than depth of ventral fin, but greater than that of dorsal fin; musculature extending to tip of tail; dorsal fin shallow anteriorly, not extending onto body; fin deepest at two-thirds its length from anterior; ventral fin deepest at midlength.

Mouth small, with a shallow lateral fold; medial portion of upper lip lacking papillae; elsewhere, papillae present in two to three rows along the border; a few papillae present medial to border in region of lateral fold; upper beak moderately deep, lower beak shallow and finely serrate; upper beak with about twelve coarse serrations medially, otherwise finely serrate; two upper and three lower rows of denticles; upper rows of same length; first upper row uninterrupted, second row broken narrowly medially; three lower rows of equal length, unbroken; denticles of first upper and third lower rows smaller than those of other rows (Fig. 7).

In life, body olive-brown above; venter silver-yellow to creamy

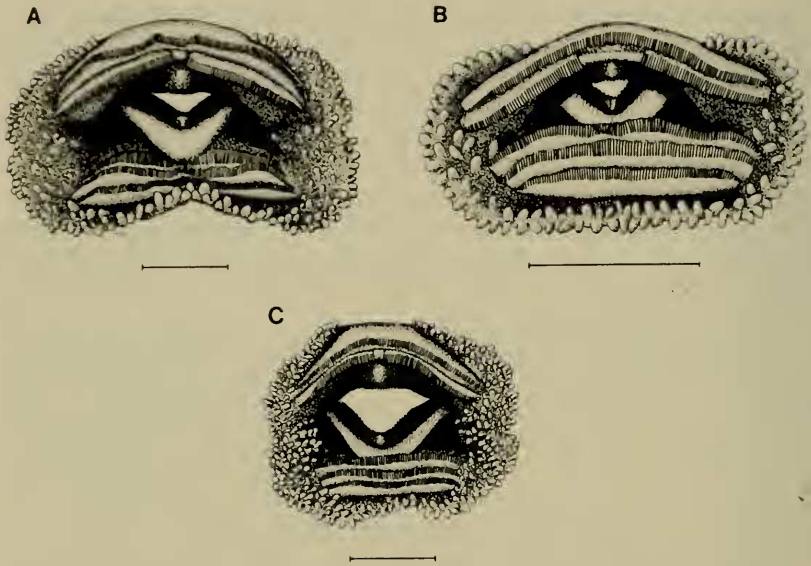


FIG. 7.—Mouths of tadpoles. A. *Phyllomedusa buckleyi*, KU 166219; B. *P. psilopygion*, KU 170213; C. *P. lemur*, USC-CRE 290-9. Line equals 2 mm.

green with greenish gold iridescence on sides; tail musculature cream to tan; fins transparent; iris silver to bronze; one metamorphic with emerging forelimbs has a green dorsum (KU 143553). In preservative, snout and top of head grayish brown; sides and venter dark bluish gray; caudal musculature dirty cream with dorsal edge of musculature dark brown; dorsal and ventral fins colorless and transparent; blood vessels easily distinguished.

One lot of tadpoles (KU 166218) has a slightly different coloration in preservative: the caudal musculature is light purple fading to reddish brown anteriorly. This may be an artifact of preservation. Another group has such an extremely heavy deposition of melanophores in the skin of the body and tail that its coloration in life was described as black. This is not unexpected, because tadpoles of *Pachymedusa dactinicolor* and *Phyllomedusa trinitatus* are known to exhibit a "tail-darkening reaction" (Bagnara, 1974).

Eggs.—The only known clutch of eggs ($n = 98$) was deposited in a plastic bag by a female (KU 143234) in amplexus. The site of natural oviposition is yet unknown, but presumably on vegetation above water. The clutch (KU 143552) was preserved at Stage 8 (Gosner); the total egg and jelly diameter is about 4.5 mm. That of the egg alone is about 3.1 mm. In life, the yolk is green; the jelly, clear.

Etymology.—The specific name is a patronym for Mr. Buckley, the collector of the holotype.

Distribution.—*Phyllomedusa buckleyi* is known from eight sites on the Amazonian slopes of Ecuador, in the drainages of the Río Coca and Río Pastaza, at elevations of 400–1870 m (Fig. 2).

Ecology.—In the valley of the upper Río Coca (Río Quijos), *P. buckleyi* occurs in lower montane rain forest. The valley is somewhat cut-over along the Quito-Lago Agrio road; temporary ponds are present in the cut-over areas and numerous small streams drain the slopes. Tadpoles of *buckleyi* have been taken from streamside pools, temporary ponds, and puddles.

In the Pastaza drainage the El Topo and Abitagua localities are lower montane rainforest; the Sarayacu site is rainforest. *Phyllomedusa buckleyi* is sympatric with *P. perinesos* in the Río Quijos Valley; in the Río Pastaza Valley *buckleyi* is sympatric with *P. vaillanti* and *P. tarsius*.

Mating Call.—No recordings of the mating call are available. However, from field observations the call is known to be a short “cluck.”

Remarks.—The holotypes of *P. buckleyi* and its two junior synonyms (*Phyllomedusa loris* and *Hyla porifera*), and one other specimen (UMMZ 92101) are from the Río Pastaza drainage. All other known specimens have been collected by University of Kansas field parties in the Río Quijos Valley. Most individuals have been taken at night on low vegetation overhanging pools of water. *Phyllomedusa buckleyi* and *perinesos* have been collected syntopically in the Quijos drainage at a site where the Quito-Lago Agrio road crosses the Río Salado. At this site twelve *perinesos* were collected on 6–7 October 1974 from bushes and tall grass in the vicinity of a small pond; no *buckleyi* were taken. On 17–19 March 1975 twelve *perinesos* were taken from low vegetation around the pond and cut-over forest at the same locality. Seven *buckleyi* were collected and low vegetation adjacent to the pond; none were taken from the cut-over forest. At this same site about 60 *perinesos* and five *buckleyi* were collected on the evening of 17 July 1977, following a light rain. All of the *buckleyi* were taken from low vegetation overhanging a small pond; the specimens of *perinesos*, including amplexant pairs, also were found around the pond, but the vast majority were in the surrounding forest clearing, several meters from water. These limited data suggest spatial segregation for the two species.

Phyllomedusa lemur Boulenger

Fig. 9

Phyllomedusa lemur Boulenger, 1882:425 [Holotype.—BMNH 74.8.11.9 (RR 1947.2.22.36) from Costa Rica].

Agalychnis lemur—Cope, 1887:15.

Agalychnis lemur—Günther, 1901(1885–1902):291.

Phyllomedusa lemur—Nieden, 1923:344.

Phyllomedusa (Agalychnis) lemur—Lutz, 1950:601,619.

Phyllomedusa lemur—Taylor, 1952:809.

Phyllomedusa lemur—Funkhouser, 1957:31.

Phyllomedusa lemur—Duellman, 1968:6.

Diagnosis.—*Phyllomedusa lemur* differs from other members of the species group by the following combination of characters: 1) modal webbing formula of foot III(3)—(4)IV(4)—(3)V; 2) calcar absent; 3) snout truncate in lateral view; 4) para-anal tubercles present; 5) outer metatarsal tubercle absent; 6) white dorsal warts absent; 7) quadratojugal present; 8) sacro-coecygeal articulation bicondylar.

Description.—Pertinent measurements and proportions in Tables 1 and 2. Head wider than body; snout short, truncate in dorsal and lateral views of both sexes; nostrils at tip of snout, directed laterally, not protuberant; internarial region flat; canthus distinct and rounded; loreal region barely concave; lips thin, not flared; interorbital region flat; eyes large and protuberant; pupil vertically elliptical; palpebrum clear; parotoid glands not differentiated; supratympanic fold barely discernible, thin and obscuring the upper edge of tympanum; tympanum round, distinct, separated from eye by distance equal to about three-fourths the diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately robust; weak ulnar fold extending from elbow to tip of fourth finger; fingers moderately long with medium size round discs; webbing, if present, very scanty (Table 5); order of fingers from shortest to longest 1-2-4-3; fingers oval in cross-section; subarticular tubercles large and round, single; supernumerary tubercles small, low and indistinct; palmar tubercle small, round and flattened; prepollex moderately enlarged, with thin horny nuptial exerescence in breeding males.

Hind limbs slender and of medium length; outer tarsal fold present, barely distinct; calcar absent, very small tubercle on heel in a few; inner metatarsal tubercle low, elliptical, not visible from above; outer metatarsal tubercle absent; toes long and slender; discs round, smaller than those on fingers; rudimentary webbing, present (Table 5); order of toes from shortest to longest 1-2-3-5-4; fifth toe with slight toe fringe; subarticular tubercles large and round; supernumerary tubercles small, indistinct, and in a single row on proximal portions of each digit.

Anus directed posteroventrally at midlevel of thighs; short anal sheath present; para-anal region and ventral surface of groin tubercular; tongue lanceolate, moderately notched from behind, free posteriorly for one-half its length; belly skin granular; skin elsewhere smooth; white dorsal warts absent; no osteoderms; vocal sac single, median, subgular, barely distensible; prevomerine teeth in some; dentigerous processes oriented posteromedially (✓), mod-

erately separated just posterior to the anterior border of elliptical choanae; vocal slits present in males, short, extending from posterolateral edge of tongue to corner of mouth.

Coloration.—In life, pale green by day; dorsal surfaces of body, forearm, fourth finger, hind limbs, and fourth and fifth toes pale green; rest of hind limb and dorsal surfaces of toes deep orange-yellow; dorsal surfaces of upper arms dark yellow; flanks orange; ventral surfaces of arms, hands and feet pinkish cream; belly creamy white; chin, upper and lower lips, outer edge of tarsi and forearms white. At night, dorsum reddish brown to lavender-brown; thighs and arms deep yellow; venter white; pale green flecks present on dorsum of some; iris silver-bronze with a black periphery.

In preservative, dorsum light bluish-gray to lavender to reddish-brown; dark brown dorsal flecks in some; hidden surfaces of limbs and ventral surfaces creamy white.

Tadpoles.—Ten tadpoles of *P. lemur* were examined, ranging from Stage 25 to Stage 41. The range of body lengths is 6.7–18.7 mm; the range of total lengths is 16.5–49.7 mm. A representative tadpole (USC-CRE 290-9) is illustrated in Fig. 6.

The following description is based on USC-CRE 290-9, a tadpole in Stage 32 with a body length of 16.0 mm and total length of 42.4 mm: body slightly wider than deep, being deepest and widest at a point two-thirds the length of the body; snout acutely rounded in lateral view; in dorsal view snout almost truncate; nostrils dorsolateral, situated one-fourth distance from eye to tip of snout, and directed anterolaterally; internarial distance equal to width of oral disc; eyes dorsolateral and directed laterally; spiracle a flap-like tube, ventral and sinistral to midline, situated at mid-length of body; chondrocranial elements not visible through skin; mouth anteroventral and small, directed anteriorly; short cloacal tube, dextral to caudal fin; slender caudal musculature tapering posteriorly gradually to end of fin; myomeres moderately differentiated; at midlength of tail the dorsal fin, ventral fin, and caudal musculature are of equal depth; dorsal fin deepest at a point two-thirds the length of the tail, and extending onto body; ventral fin of uniform depth anteriorly, deepening slightly just posterior to the midlength of the tail and tapering gradually to the tip.

Mouth small, with a slight lateral fold; median portion of upper lip lacking papillae; elsewhere mouth bordered by two to three rows of papillae; papillae densely packed in lateral fold region; upper beak moderately deep; lower beak shallower; medial portion of upper beak edge with about twelve coarse serrations; lower beak and lateral portions of upper beak finely serrate; two upper and three lower rows of denticles; first upper and third lower rows with fine denticles; remaining rows with coarse denticles; upper rows of equal length, the second being interrupted medially; lower rows

unbroken and shorter than upper rows; lower third row shorter than other two (Fig. 7).

In preservative, top of head brown; sides and venter purplish pink; caudal cream; sides, venter, and tail with brown flecks and mottling; tail fins transparent, with some brown flecks in anterior portion of dorsal and ventral fins.

Eggs.—No clutches of eggs were available for examination. A color transparency (KU 1417) of a clutch of presumably *Phyllomedusa lemur* eggs from Tapantí, Costa Rica, demonstrates a clutch size of about 70. The eggs are arranged in a single layered mass in the central portion of the upper surface of a leaf. Van Eijsden (1977) reported clutch sizes in captivity of 23 and 25 eggs.

Etymology.—The specific name is a noun in apposition, in reference to the lemur-like locomotion of the species.

Distribution.—The species is found primarily on the Caribbean slopes of the Cordilleras de Tilarán, Central, and Talamanca in Costa Rica; from the Atlantic and upper Pacific slopes of the Cordillera de Talamanca, and the southern slopes of the Serranía de Tabasará, on Cerro Malí and Cerro Tacarcuna in Panamá. The species ranges from elevations of 440 to 1600 m (Fig. 1).

Ecology.—*Phyllomedusa lemur* is generally considered to be restricted to the Subtropical Life Zone of Holdridge (Savage and Heyer, 1969). In Costa Rica the biotemperature of this zone is 18–24° at altitudes of 500–1500 m. The species is part of the Caribbean versant fauna in Costa Rica; the localities around Monteverde and La Palma are on the upper Pacific slopes, virtually on the continental divide where the biota is essentially an “overflow” from the Caribbean slopes. Collections from Tapantí, while properly south of the Cordillera Central, are nonetheless in the Atlantic drainage of the Río Reventazón. All other localities in Costa Rica are clearly in Atlantic drainages.

Records of the species in Panamá are sparse and widespread, and the ecological distribution requires some explanation. Collections from the western province of Bocas del Toro are from Caribbean versant lower montane rainforest. In western Panamá the species is found also on the Pacific slopes, at the Fortuna Dam site on the upper Río Chiriquí, Provincia de Chiriquí. The upper Chiriquí Valley can be considered Temperate Wet (Cf) under the Köppen system, as opposed to the Temperate Wet and Dry climate (Cw) that is characteristic of most of the Pacific versant, including the lower drainage of the Río Chiriquí. The dam site receives about 4000 mm of rain annually and lacks a dry season. In addition, the herpetofauna of the upper Chiriquí reflects a greater zoogeographic affinity to the Caribbean, rather than the Pacific assemblage (Charles W. Myers, pers. comm.). The exceptional climate and herpetofauna can be explained by noting that the upper Chiriquí

Valley structurally divides the central cordillera, marking the western end of the Serranía de Tabasará and eastern extent of the Cordillera de Talamanca. In this depression the continental divide drops below 1200 m. In effect, the climate and herpetofauna spill over onto the Pacific slopes.

A second noteworthy occurrence of *Phyllomedusa lemur* is on the south slope of Cerro Campana and at El Valle, a low Pleistocene volcanic crater about 20 km SW of Cerro Campana. Again, a seasonally dry forest is associated with the Pacific drainages of this region. However, Cerro Campana is the eastern terminus of the central cordillera, and the absence of nearby high mountains allows the 1000 m peak and the surrounding area to intercept the northeasterly Caribbean winds, with the resultant orographic rainfall. Thus the upper Pacific slopes near El Valle and Cerro Campana support a humid subtropical cloud forest (Myers, 1969).

The easternmost extent of *Phyllomedusa lemur* is the drainage of the Río Tuira, on the slopes of Cerro Malí and Cerro Tacarcuna. The species is unknown from the Caribbean side of the Serranía del Darién; thus the Río Tuira sites, in humid montane forest, are the only records of the species in an exclusively Pacific drainage. The species is not known from Colombia.

Mating Call.—The mating call of *Phyllomedusa lemur* is a very short trill. A recording from La Palma, Costa Rica (KU Tape 67), at an air temperature of 17.8°C, consists of four calls in a period of 99 seconds. The call duration is 0.32–0.40 seconds. The fundamental frequency is 250–300 Hertz; the dominant frequency is about 950–1000 Hertz. The call is poorly modulated; harmonics can be distinguished at 1350, 1900, and 2200 Hertz. The pulse rate is 39–41 pulses per second (Fig. 10).

Remarks.—Van Eijsden (1977) and Schulte (1977) provided observations on *P. lemur* in captivity.

Phyllomedusa medinai Funkhouser

Fig. 9

Phyllomedusa medinae Funkhouser, 1962:588 [Holotype.—EBRG (no number) from Parque Henri Pittier, Rancho Grande, Estado de Aragua, Venezuela].

Phyllomedusa medinae—Duellman, 1968:6.

Diagnosis.—*Phyllomedusa medinai* differs from other members of the species group by the following combination of characters: 1) modal webbing formula of foot I(2+)—(2.25)II(2+)—(3.5)III(2+)—(3.5)IV(3+)—(2+)V; 2) calcar absent; 3) snout sloping in lateral view; 4) para-anal tubercles present; 5) outer metatarsal tubercle sometimes present; 6) white dorsal warts sometimes present; 7) quadratojugal absent; 8) sacro-coccygeal articulation bi-condylar.

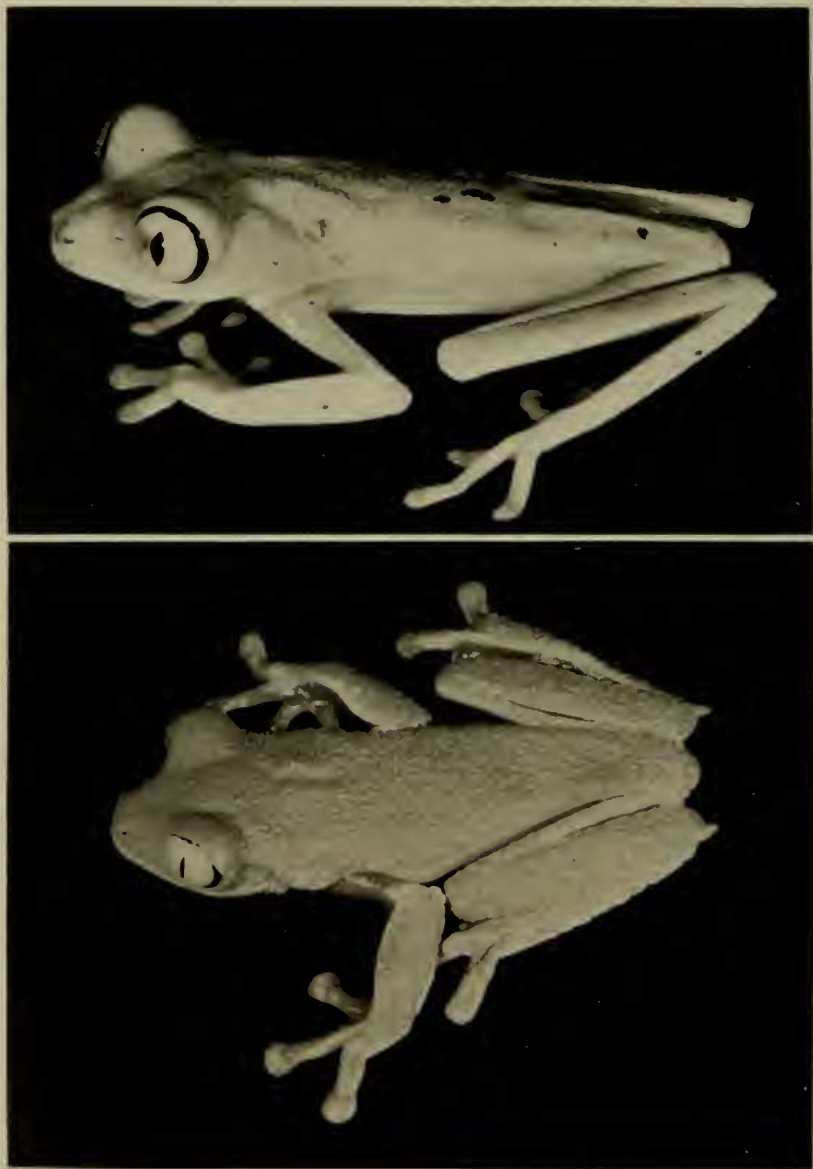


FIG. 8.—Top: *Phyllomedusa psilopygion*, male, holotype, SVL 42.0 mm, KU 169608. Bottom: *P. buckleyi*, male, SVL 43.4 mm, KU 143225. Photos by William E. Duellman.

Description.—Pertinent measurements and proportions in Tables 1 and 2. Head slightly wider than body; snout short, acutely rounded in dorsal view; intermediate between truncate and sloping in lateral view in both sexes; nostrils at tip of snout, directed later-

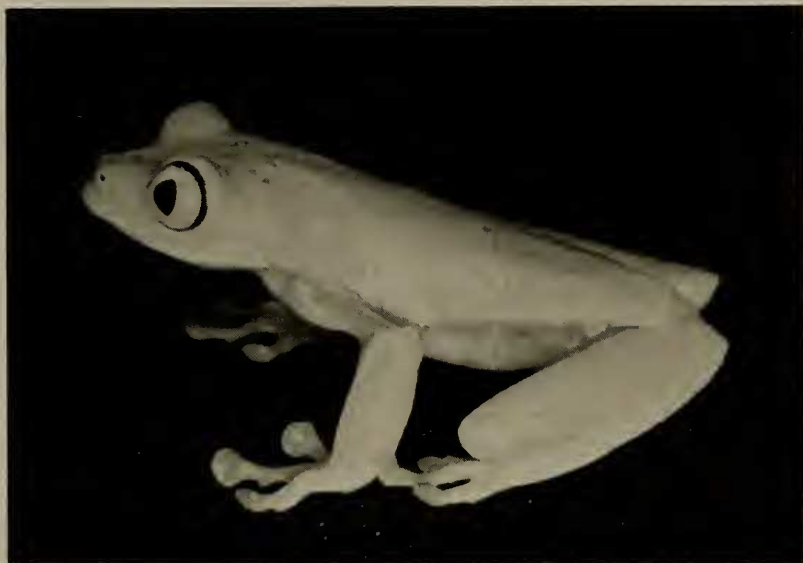


FIG. 9.—Top: *Phyllomedusa medinai*, male, SVL 43.2 mm, KU 167186. Bottom: *P. lemur*, female, SVL 43.7 mm, AMNH 94915. Photos by William E. Duellman and Charles W. Myers, respectively.

ally, not protuberant; internarial region slightly concave; canthus rounded, distinct; loreal region barely concave; lips thin, not flared; interorbital region flat; eyes large and protuberant; pupil vertically

elliptical; palpebrum clear; parotoid glands not differentiated; supratympanic fold thin, obscuring dorsal and posterior edge of tympanum, extending posteroventrad to angle of jaw; tympanum round, distinct, separated from eye by distance equal to one-half diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately robust, stouter in males; slight ulnar fold extending from elbow to disc of fourth finger; fingers short; discs of moderate size, rounded; order of fingers from shortest to longest 1-2-4-3; fingers flattened in cross section; no finger fringe; distal subarticular tubercles oval, subconical, large and single; proximal subarticular tubercles more rounded and smaller; supernumerary tubercles small and few in number, in a single row on proximal portions of digits; palmar tubercle diffuse; prepollex moderately developed, with thin horny nuptial excrescence in breeding males; small amounts of webbing between fingers (Table 5).

Hind limbs slender and moderately long; weak tarsal fold extending from heel to pad of fourth toe; calcar absent; outer metatarsal tubercle present in some; inner metatarsal tubercle flat, oval, small, not visible from dorsal view; toes moderately long, with rudimentary webbing (Table 5); discs rounded, smaller than those on fingers; distal subarticular tubercles single, medium size, subconical; proximal subarticular tubercles smaller and less distinct; supernumerary tubercles very few in number, small and rounded; order of toes from shortest to longest 1-2-3-5-4.

Anus directed ventrally at lower level of thighs, covered by short anal flap; para-anal tubercles present; skin on belly and ventral surface of groin finely granular; skin on anterior part of body slightly granular, with granules becoming better defined on dorsal surface of hind limbs and posterior dorsum; skin smooth elsewhere; white dorsal warts present in some specimens; no osteoderms; tongue lanceolate, slightly notched, free posteriorly for one-third to one-half of its length (tongue round, not notched, not free in CAS-SU 21828); prevomerine teeth present in about one-half of the specimens; dentigerous processes moderately separated, located midway between anterior and posterior levels of elliptical choanae, oriented posteromedially (\setminus); vocal sac single, median, and subangular; vocal slits present in males, short, extending from corner of mouth anteriorly toward posterolateral corner of tongue.

Coloration.—In life, dorsum pale green by day; at night, reddish brown with rusty red flecks; ulnar and tarsal strips creamy white; chest and throat white; belly, other ventral surfaces, upper portions of limbs, hands and feet orange; iris pale silvery bronze.

In preservative, dorsal surfaces of head, body, limbs, portions of fourth finger and fourth and fifth toes dark lavender in recently preserved specimens, reddish brown to cream in faded specimens;

upper edge of palpebrum pigmented; brown flecks present on dorsum of all specimens; white dorsal warts in most; ventral and concealed surfaces, and dorsal surfaces of fingers and toes creamy white.

Tadpoles and Eggs.—The tadpoles and eggs mentioned in Funkhouser (1962) apparently are lost. However, Dr. Anne Funkhouser has kindly provided me with an unpublished manuscript on phyllomedusine tadpoles from which is taken the following description, based on larvae from a single clutch of about 150 eggs:

“Eggs. gelatinous coat 6 mm, egg proper 2 mm, pale blue.

“Tadpoles. Newly hatched larvae (11 mm) still have long external gills which become covered by the operculum within a day after hatching. There is large amount of yolk present, and feeding does not begin until several days after hatching.

“In 18 mm tadpoles the body length is one-third or less the total length; body oval in outline when viewed from above; deeper than wide. Eyes lateral, prominent. Nostrils subterminal. Spiracle ventral and slightly sinistral to longitudinal body axis; opening slightly closer to base of tail than to snout. Anus median. Tail at least twice body length; fins broadest at midpoint, terminating posteriorly in a pointed tip. Dorsal fin not extending onto body.

“Mouth terminal. Single papillary border around mouth incomplete above. Beaks broadly arched; lower more well-developed than upper. Labial denticles 1/2; upper and first lower interrupted medially; set on folds of skin.

“In life somewhat iridescent; uncolored except for scattered black pigment at front of head, along tail musculature and as a conspicuous inner covering of the abdominal cavity. Iridescence lost with preservation.”

The labial denticle formula recorded above is associated with an obviously young tadpole. I would predict that a more advanced tadpole of *P. medinai* would have the normal phyllomedusine denticle formula of 2/3.

The only apparent extant larval specimen of *medinai* (KU 179406) is a single metamorphic young at Stage 43 with a SVL of 23.0 mm and total length of 44.6 mm. The adult pattern of webbing is fully developed between the fingers and toes. In preservative, the dorsal surfaces are light gray-brown with several dark brown spots on the dorsum. The venter is pale gray.

Funkhouser (1962) noted that the colubrid snake *Leimadophis zweifeli* preys on the eggs of *P. medinai*.

Etymology.—The specific epithet is a patronym for the collector, Sr. Gonzalo Medina Padilla.

Distribution.—*Phyllomedusa medinai* is known only from the type locality, Rancho Grande, Venezuela, 1100 m (Fig. 2).

Ecology.—Little is known of the habits of this cloud forest

dweller. Two specimens (KU 167186-7) were taken on vegetation 20-30 cm above ground at night. The range of temperatures at this time (2-12 August 1974) was 17.0-26.0° C; rainfall averaged 13.8 mm per day with a range of 0-54 mm.

Mating Call.—The mating call of the species is unknown.

Remarks.—The Estación Biológica Rancho Grande is on the southern slope of the coastal (northern) arm of the Cordillera de la Costa (Caribbean range of the Andes) at an elevation of 1100 m. Within 200 m of the site is a narrow pass, Portachuelo, bordered on the east by Pico Guacamayo (1900 m), and on the west by Pico Periquito (1500 m). The station, noted simply as Rancho Grande on maps, is part of the Parque Nacional Henri Pittier, a largely undisturbed region. Rancho Grande lies in an ecologically transitional zone (Test, Heatwole, and Sexton, 1966). The station is at the lower limit of cloud forest on the southern face of the divide; below the cloud forest there is a warmer, drier, semi-deciduous vegetation zone. June, July, and August are the wettest months; January, February, and March have only traces of rain.

Rivero (1967) suggested that since the species was named in honor of Gonzalo Medina, the spelling of the trivial name as *medinae* was a *lapsus calami* by Funkhouser. He implied that the specific epithet should be spelled as *medinai*, but due to either a topographical error or *lapsus calami* on his part he again spelled it *medinae*. According to the 1961 Code—in effect at the time the species was described—a species-group name formed from the personal name of a man must end in *-i* (Article 31). The spelling of the specific epithet as *medinae* is an incorrect original spelling and must be corrected (Article 32). The name is emended here to *medinai*.

Phyllomedusa psilopygion new species

Fig. 8

Holotype.—KU 169608, an adult male, from 8 km W Danubio, Río Anchicayá, Departamento de Valle, Colombia, 300 m, [03°37'N, 76°47'W], obtained on 12 June 1975, by William E. Duellman.

Paratopotypes.—KU 169609-13, William E. Duellman, 12-14 June 1975; ICN 4755, Craig Downer, 3 August 1978.

Paratype.—AMNH 87873 from Quebrada Guanguí, Río Patia, in the Río Saija drainage, Departamento de Cauca, Colombia, c. 100 m, obtained on 29 October 1971, by Adriano Granja and Borys Malkin.

Diagnosis.—*Phyllomedusa psilopygion* differs from other members of the species group by the following combination of characters: 1) modal webbing formula of foot III(3-)-(4)IV(4-)-(3-)V; 2) calcar present; 3) snout truncate in lateral view; 4) paranasal tubercles absent; 5) outer metatarsal tubercle absent; 6) white

dorsal warts sometimes present; 7) quadratojugal present; 8) sacrococcygeal articulation fused.

Description.— $N = 6 \text{ } \delta \text{ } \delta$, $2 \text{ } \text{♀} \text{ } \text{♀}$; pertinent measurements and proportions in Tables 1 and 2. Head slightly wider than body; snout short, truncate in lateral view, acutely rounded in dorsal view of both sexes; nostrils at tip of snout, not protuberant, directed laterally; internarial region flat; canthus rounded; loreal region barely concave; lips thin and not flared; interorbital region flat; eyes large and protuberant; pupil vertically elliptical; palpebrum clear; parotoid glands not differentiated; supratympanic fold thin, obscuring dorsal and posterior edge of tympanum, extending posteroventrad to angle of jaw; tympanum round, distinct, separated from eye by distance equal to one-third diameter of tympanum.

Axillary membrane absent; upper arm slender; forearm moderately developed, with weakly developed ulnar fold extending from elbow to disc of fourth finger; fingers of moderate length, not webbed; discs rounded and small; fingers flattened in cross section; slight finger fringe present on either side of digits; order of fingers from shortest to longest 1-2-4-3; distal subarticular tubercles barely rounded and elevated; tubercle on fourth finger slightly bifid; supernumerary tubercles small, flattened, present proximally; palmar tubercle diffuse, single; prepollex moderately developed, with thin horny nuptial excrescence in breeding males.

Hind limbs slender and moderately long; weak outer tarsal fold extending from small calcar and merging with toe fringe of fifth toe; inner tarsal fold very weak; outer metatarsal tubercle absent; inner metatarsal tubercle flat, elliptical, not visible from above; toes of moderate length, webbed basally (Table 5); discs rounded, smaller than those on fingers; toe fringe present, widening distally; subarticular tubercles large, rounded, flattened on the more distal segments; supernumerary tubercles small and indistinct; order of toes from shortest to longest 1-2-3-5-4.

Anus directed posteroventrally at midlevel of thighs, covered by short anal flap; tubercles absent on para-anal region; skin on belly and ventral surface of groin faintly granular, smooth elsewhere; white dorsal warts present in some; no osteoderms; tongue lanceolate, slightly notched from behind, free posteriorly for one-third of its length; prevomerine teeth present; dentigerous processes oriented posteromedially (∇), moderately separated at level of anterior margins of elliptical choanae; vocal sac single, median, subgular; vocal slits present in males, short, extending from posterolateral corner of tongue to corner of mouth.

Coloration.—In life, at night, dorsum dull green to reddish brown with green flecks; by day, pale green with or without reddish brown flecks; dorsal warts creamy yellow; flanks, upper arms, anterior and posterior surfaces of thighs, fingers 1-3, toes 1-4, and

ventral surfaces of hind limbs bright orange; throat, belly, anal region and ventral portion of forearms white; tarsal stripe and elbow pale gray; iris creamy white; palpebrum clear.

In preservative, dorsal surfaces of head, body, limbs, fourth fingers and fourth and fifth toes dark lavender brown, some with splotches of bluish gray and pink; dorsal warts white; ventral and concealed surfaces and dorsal surfaces of fingers 1-3 and toes 1-4 creamy white.

Tadpoles.—A lot of fifteen tadpoles (KU 170213), all at Stage 25, was examined. The mean body length is 11.8 mm (range, 8.5-17.9); the mean total length is 29.4 mm (range, 24.1-40.4). A typical tadpole with body length of 17.9 mm and total length of 40.4 mm is illustrated in Fig. 6.

Body slightly wider than deep; snout acutely rounded in lateral profile; in dorsal view snout almost truncate; body widest and deepest at two-thirds length of body; nostrils dorsolateral, directed anterolaterally, situated at end of snout; internarial distance equal to width of oral disc; eyes dorsolateral and directed laterally; spiracle a flap-like tube, ventral and sinistral to midline; spiracular opening at a point slightly more than one-third length of body from anterior end; skin transparent; chondrocranial elements visible through dorsal skin of head; mouth anteroventral and directed anteriorly; cloacal tube short and dextral to caudal fin; caudal musculature slender, tapering distally to end of fin; myomeres poorly differentiated; ventral fin deepest just posterior to body and tapering gradually to tail tip; dorsal fin narrow anteriorly, widening to its deepest at midlength of tail; dorsal fin never as deep as ventral fin in the same vertical transect; dorsal fin not extending onto body.

Mouth small, without lateral fold; upper lip lacking papillae medially; otherwise, papillae present in one row laterally and two rows ventrally along border; very few present elsewhere; upper and lower beaks shallow, both with small uniform serrations; two upper and three lower rows of denticles; second upper row interrupted medially; upper rows of equal length; lower rows unbroken and not as long as upper rows; third lower row shorter than others; denticles on first upper and third lower rows finer than those of other rows (Fig. 7).

In life, body reddish brown above with gold flecking below; tail bluish gray; smaller individuals nearly pigmentless; iris pale bronze. In preservative, dorsal surface brown; sides lighter brown, almost transparent with a slight metallic blue sheen; caudal fins transparent; larger tadpoles having dark brown pigment along dorsal edge of caudal musculature and tail fin in the anterior half of tail; posterior one-fourth of tail fin without pigment.

Eggs.—A single clutch of eggs (KU 170214), presumably of this species, is available for examination. The clutch ($n = 32$) is em-

bedded in a single gelatinous matrix; the eggs are at Stage 16; the diameter of the eggs averages 4.3 mm. In life the yolk is grayish tan; the jelly, clear.

Etymology.—The specific epithet is derived from the Greek *psilos*, meaning smooth or bare, and the Greek *pyge*, f., meaning rump; *pygion* is the neuter diminutive form. The epithet *psilopygion* is a noun in apposition, applied in reference to the lack of para-anal tubercles, which are possessed by other species in the group.

Distribution.—*Phyllomedusa psilopygion* is known only from elevations of 100 and 300 m on the Pacific lowlands of southern Colombia (Fig. 2).

Ecology.—The type series was collected in an area of steep slopes covered with rainforest. Some males were found calling from bushes and tangled vines at the mouth of a natural grotto at night. Tadpoles were collected from the same grotto by Linda Trueb, and John E. Simmons found the clutch of apparently phyllomedusine eggs on the underside of a rock protruding from the side of the grotto.

During the period 10–14 June 1975 the range of temperatures at the locality was 21.0–32.0° C; the average rainfall was 4.5 mm with a range of 2.0–9.5 mm.

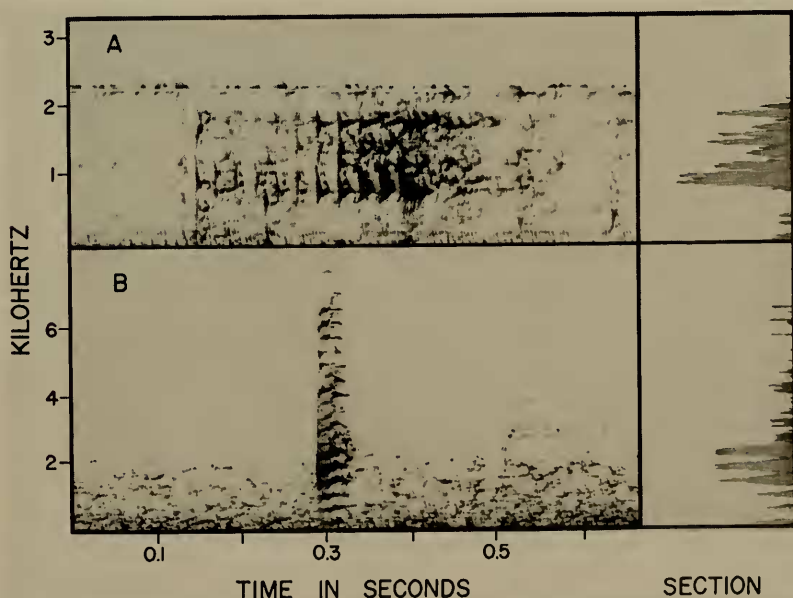


FIG. 10.—Audiospectrograms of mating calls. A. *Phyllomedusa lemur* (KU Tape 67). B. *P. psilopygion* (KU Tape 1350).

Mating Call.—The call of *P. psilopygion* consists of a single chirp. At the type locality on 13 June 1975, five calls were recorded during a period of 143 seconds from KU 169611 (KU Tape 1350) at an air temperature of 23° C at 2130 h. The call duration is 0.04–0.05 seconds. The fundamental frequency is about 250 Hertz; the dominant frequency, 1900 Hertz. The well-modulated call has distinguishable harmonics at about 250, 700, 1100, 1500, 1900, 2300, 2700, 3200, 3600, 4000, and 4800 Hertz, with the most intense frequencies at 1500, 1900, and 2300 Hertz (Fig. 10).

Remarks.—The type locality is on the grounds of the Central Hidroeléctrica de Anchicayá generating facility. One paratype (AMNH 87873) was taken in the drainage of the Río Saija, about 120 km SW by air from the type locality (See Myers and Daly, 1976, for map). This paratype differs from the type series only by the apparent absence of a small calcar on the heel, but the limbs are strongly flexed at the heels, where the skin is stretched and possibly abraded slightly. In addition, some individuals of species normally having small calcars (e.g., *P. buckleyi*) do lack them.

BIOGEOGRAPHY

The most cogent biogeographical analyses are those that are based on a hypothetico-deductive model; such hypotheses have the potential to be tested and falsified. A choice between competing hypotheses therefore will have a logical basis. The formulation of such biogeographical hypotheses requires a cladistic analysis of the group under study (Ball, 1975). At present, the lack of data on other phyllomedusines precludes the formation of a hypothesis of relationships within the *buckleyi* group. It has been noted in previous sections that *buckleyi* and *medinai* are superficially most similar to each other; *lemur* and *psilopygion* closely resemble each other. Overall phenetic similarity is not necessarily indicative of relationship, however. Thus, a deductive analysis of the biogeography of the group is not feasible. It is of heuristic value to describe the general patterns of distribution in the group, however. The four allopatric species are isolated from one another by various segments of the Andean cordillera. A parsimonious explanation that does not invoke unnecessary dispersal is that the Andean orogeny dissected a previously widespread species in northwestern South America. Possibly this stock was present in the early Pliocene, when the northern Andes lay in a tropical belt with the greatest elevation not over 1000 m (Van der Hammen, 1974). The major uplift of the cordillera at the end of the Pliocene fragmented the stock; further differentiation may have occurred in Pleistocene refugia (Simpson, 1975; Haffer, 1970). It is worth noting that the presence of *P. medinai* in the Cordillera de la Costa of Venezuela provides a link of this region to the rest of the Andes; the herpeto-

faunal similarity between the Cordillera de la Costa and the Andes of Colombia is very low (Duellman, pers. comm.).

It is significant that other groups of montane anurans display similar distribution patterns in northwestern South America. *Hemiphractus*, *Rhampophryne*, the *Hyla bogotensis* group, and the *Gastrotheca cornuta* group have patterns that suggest that a formerly widespread biota was divided by the Andean orogeny. For distributional analyses of these groups see Duellman (1972) and Trueb (1971, 1974).

RESUMEN

El grupo *buckleyi* del género *Phyllomedusa* está compuesto por cuatro especies. Una de ellas descrita aquí como nueva: *Phyllomedusa psilopygion*, de la selva de la región de Chocó en Colombia, en el valle del Río Anchicayá (Departamento de Valle) y del Río Patía (Departamento de Cauca). De las otras especies, *Phyllomedusa lemur* es conocida de las laderas caribes de Panamá y Costa Rica; *P. buckleyi* se encuentra en las laderas amazónicas del Ecuador, y *P. medinai* es conocida sólo de Rancho Grande, Estado de Aragua, Venezuela. Las especies habitan selvas húmedas de 100 m hasta 1870 m de altitud. Miembros del grupo *buckleyi* difieren de las otras especies de la subfamilia Phyllomedusinae por la combinación siguiente de caracteres:

- 1) Membrana de manos y pies menos de un cuarto del longitud del dedo.
- 2) Primer dedo posterior más corto que el segundo.
- 3) Glándula parótida no diferenciada.
- 4) Párpado inferior sin reticulación.
- 5) Flancos anaranjados (especímenes vivos) sin barras ni manchas.
- 6) Ramo posterior (*pars scapularis*) del músculo *depressor mandibulae* ausente.

Phyllomedusa perinesos no es miembro del grupo *buckleyi*.

Los renacuajos del grupo tienen cuerpos ovalados, con aletas de altura moderada, boca anteroventral, dos filas superiores y tres filas inferiores de denticulos. Papilas labiales faltan en la región mediana del labio superior. Los renacuajos son similares a los de *Agalychnis*, *Pachymedusa*, y algunos de *Phyllomedusa*. Los huevos sin pigmento son depositados en la vegetación (o piedras) encima de aguas lénticas.

SPECIMENS EXAMINED

Phyllomedusa buckleyi

ECUADOR: Napo: South Slope Cordillera del Dué. Río Coca, 1150 m [00°02'S, 77°33'W], KU 121445-9; Río Azuela, 1740 m [00°07'S, 77°37'W], KU 143226-36, 143234 (skeleton), 143550-1 (tadpoles), 143552 (eggs), 143553 (tadpoles), 166217 (tadpoles), 164443; Río Salado, \pm 1 km upstream from Río

Coca, 1410 m [00°13'S, 77°44'W], FMNH 204287, KU 166218-9 (tadpoles), 164444-8, 164449 (skeleton), 178848-50, 179404-5 (cleared and stained); 4.7 km N Santa Rosa, 1870 m, KU 143549 (tadpoles); 16.5 km NNE Santa Rosa, 1700 m, KU 143225. *Pastaza*: Abitagua (8 km NW Mera), 1300 m [01°26'S, 78°07'W], UMMZ 92102.

Phyllomedusa lemur

COSTA RICA: *Alajuela*: Cariblanco, 830 m, MCZ 7966; Cinchona, 1600 m, FMNH 172156, KU 35896-7, 63993-8, 68575 (tadpoles); Isla Bonita, c. 1500 m, FMNH 101749, 174823; La Balsa, KU 140015; 4.8 km S Ciudad Quesada, 1000 m, USC-CRE 8077. *Cartago*: Bridge over Río Grande at Tapantí, 1201 m, USC-CRE 2640; El Silencio de Sitio Mata, La Suiza, 1200 m, USC-CRE 234; 9.9 km NE (by road) Bridge over Río Reventazón-Road from Turrialba to Peralta, Río Chitaría, 775 m, USC-CRE 6141; Moravia de Chirripó, 1116 m, KU 31720 and 31722 (skeletons); Moravia de Turrialba, 1116 m, KU 31700-19 (31703, 31707, 31719, cleared and stained), 31774; Tapantí, 1170-1300 m USC-CRE 6295, 6309(6), MCZ 75353, UMMZ 129202(5), KU 63940-92 (63973, cleared and stained), 68626-9 (cleared and stained). *Limón*: Confluence of Ríos Lari and Pari about 20.8 km SW Amubri, 440 m, USC-CRE 7178; El Tigre, 9-14 km from Siquirres on Petrolera road to Turrialba, 680 m, KU 70026 (tadpoles), USC-CRE 290-9(3), 290-5 (tadpoles), 290-9(2) (tadpoles), 290-11 (tadpoles). *Puntarenas*: 3.6 km E Monteverde, 1550-1580 m, USC-CRE 7206; Vicinity Monteverde, Crest of Sierra de Tilarán, 1600 m, UMMZ 126616. *San José*: Bajo La Hondura, Trail to Río Claro, 1150-1250 m, USC-CRE 9802-4; Confluence of Río Claro and Río La Hondura, 1128-1189 m, USC-CRE 7048(9), 7048(2) (tadpoles), 8081; 1.4 km S Alto La Palma, 1500 m, USC-CRE 7034(9), 7144(7); 1.1 km W La Hondura, 1128 m, USC-CRE 7035(2); La Hondura, 1245 m, MCZ 75351-2; Vicinity La Palma, 1500 m, USC-CRE 490(2), 502(5), 510, 527(4), 6208-11; La Palma, c. 1450 m, KU 63999-64013, 86506, MCZ 7921-2, UMMZ 122666(2), 122667(3), 129201, USNM 75066; Río Claro on La Palma-Carrillo road, 1188 m, USC-CRE 6311.

PANAMÁ: *Bocas del Toro*: Río Changena, 650 m [09°00'N, 82°34'W], KU 101813-6 (101815, cleared and stained); Río Changena, 830 m [09°00'N, 82°36'W], KU 101817; Río Changena, 35.2 km W Almirante, 650 m, BYU 19143-4; Río Claro, near junction with Río Changena, 910 m [09°00'N, 82°37'W], KU 101818-24 (101818 and 101823, cleared and stained). *Chiriquí*: Upper Río Chiriquí, Fortuna Dam Site, 1000 m [08°40'N, 82°20'W], AMNH 94915-7, 94918 (cleared and stained). *Coclé*: El Valle, 560 m [08°36'N, 80°08'W] (literature record; Duellman, 1970). *Darién*: Cerro Malí, 1250 m, USNM 151079; Cerro Malí, 1380 m [08°07'N, 77°13'W], AMNH 90988-9; South Base of Cerro Tacareuna, Río Pucro, 640 m [08°06'N, 77°15'W], AMNH 90990; *Panamá*: Cerro Campana, 800 m, AMNH 84910-1 (metamorphic young); Cerro Campana, 850 m [08°41'N, 79°56'W], KU 77496-8, UMMZ 131091.

Phyllomedusa medinai

VENEZUELA: *Aragua*: Estación Biológica Rancho Grande, 1100 m [10°22'N, 67°42'W], CAS-SU 20379 (paratype), 21827-8, KU 167186-7, 179407 (cleared and stained), 179406 (metamorphic young), MCZ 65965.

Phyllomedusa psilopygion

COLOMBIA: *Cauca*: Quebrada Guanguí, Río Patia, in Río Saija drainage, c. 100 m, AMNH 87873. *Valle*: 8 km W Danubio, Río Anchicayá, 300 m